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FIGHTING IN FEMALE MAGELLANIC PENGUINS: WHEN, WHY, AND WHO WINS?

DANIEL RENISON,[1,3] DEE BOERSMA,[2] AND MÓNICA B. MARTELLA[1]

ABSTRACT.—Female Magellanic Penguins (*Spheniscus magellanicus*) fought for the best quality nests, mainly before egg laying. Female fights (n = 47) were longer than male fights (n = 138), but less frequent and less intense as indicated by the number of flipper hits and length of cuts. Female winners occupied the disputed nests, and losers usually moved to nests of lower quality. Losers subsequently fledged fewer chicks than winners. Female winners were in better body condition, were not significantly larger, and were the owners of the nest as indicated by previous season attendance at the nest. *Received 17 April 2002, accepted 22 September 2002.*

Aggression among female birds is less studied than among males; however, several studies suggest that female aggression could be widespread in birds (Yasukawa and Searcy 1982, Rätti et al. 1994, Liker and Székely 1997, Sandel and Smith 1997) and could affect mating systems and parental care (Liker and Székely 1997). Female birds fight for nests or territories (Chek and Robertson 1991), for mates (Stephens 1982, Freed 1986, Hotta 1994), to exclude other females from laying eggs in their nests (Møller 1987), or to avoid sharing their mate (Yasukawa and Searcy 1982, Liker and Székely 1997, Sandel and Smith 1997).

Game theory models predict that the willingness of individuals to fight should vary according to the value of winning a resource. Females therefore should be more aggressive when the potential benefits of winning are relatively high (Maynard Smith and Parker 1976, Hammerstein 1981, Parker and Rubenstein 1981, Hammerstein and Parker 1982). Furthermore, game theory models suggest arbitrary rules such as "owners win" could be an evolutionarily stable strategy (ESS) when the benefits of winning a fight are low relative to fighting costs (Maynard Smith and Parker 1976). When payoffs of winning are high for at least one of the contestants an ESS is unlikely, because individuals that break the rules benefit. Thus, when payoffs are high models predict disputes should be determined by asymmetries in fighting ability (also known as resource holding potential) or asymmetries between contestants in the value of the disputed resources (Parker 1974, Maynard Smith and Parker 1976, Enquist and Leimar 1983, Leimar and Enquist 1984). When asymmetries in fighting ability or resource value are used to settle contests, individuals should evaluate these asymmetries during the fight and use this information to determine whether to retreat and avoid further injury, or to continue fighting. As a consequence, when differences in fighting ability between contestants and differences in how the individuals value the disputed resources are small, fight duration should increase (Parker 1974, Enquist and Leimar 1983).

We describe fights between female Magellanic Penguins (*Spheniscus magellanicus*) and assess the predictions of game theory models that the benefits of winning determine the outcome and severity of fights. Magellanic Penguins are colonial monogamous seabirds in which both mates incubate eggs, brood small chicks, and feed them until they fledge (Boersma et al. 1990). They breed in nests dug in the soil or under bushes, and having a poor quality nest reduces fitness (Stokes and Boersma 1998). Female Magellanic Penguins are seen at the colony less frequently than males and thus we expected nest acquisition to be less competitive for females than for males. We expected that the strategy "owners win" should have a higher chance of being evolutionarily stable in female than in male Magellanic Penguins because the cost of losing is less for females. Our study (1) examined why females fight; (2) compared the fighting behavior of females with males; and

[1] Centro de Zoología Aplicada, Univ. Nacional de Córdoba, C.C. 122, 5000 Córdoba, Argentina.

[2] Wildlife Conservation Society, Dept. of Zoology, Univ. of Washington, Seattle, WA 98195-1800, USA.

[3] Corresponding author; e-mail: drenison@com.uncor.edu

(3) determined whether body size, physical condition, or ownership predicted who won female fights.

METHODS

The largest breeding colony of Magellanic Penguins is located at Punta Tombo, Argentina (44° 02′ S, 65° 11′ W). From September 1992 through January 1996 we watched for fighting penguins in a study area within the colony that was mainly devoid of vegetation and had a density of 20–30 nests/100 m^2 (Stokes and Boersma 2000).

We watched during most of the four breeding seasons approximately 2,000 nests for a total of 463 h. We observed primarily during the early morning and late afternoon, when penguins were most active (Renison et al. 2002). A fight was considered to start when two birds mutually pecked or flipper hit each other, and ended when contestants lost contact for ≥5 min. We recorded fight duration and counted the total number of flipper hits (we were unable to differentiate who received and who gave flipper hits). The sum of the length of cuts on each opponent was measured to the nearest mm.

After a fight, we marked the contested nest, captured both contestants, and banded them with stainless steel flipper bands. We measured bill length and depth, and flipper and foot length (see Boersma 1974). We determined the sex of fighters by body measurements (Scolaro et al. 1983), patterns of pairing and arrival to the colony (Boersma et al. 1990), and visual examination of their cloacas (Boersma and Davies 1987).

We systematically visited all nests in the study area to find females once in early October when most birds were in the colony, and in mid-October when females were incubating. In addition, we searched for contestants by walking around the area for ≥20 min every 2–8 days from September through mid-February. We may have missed some females that lost their eggs early, but females that fledged chicks were likely to be found.

We marked nests with female contestants and visited them every 4–15 days during the breeding season to determine nest contents. We measured the length and width of the eggs and we calculated an egg volume index by multiplying length by $width^2$. Chicks were individually marked and were considered to have fledged if they were alive after January 8 and their mass was ≥1.8 kg (Boersma et al. 1990). We considered a female the parent of the eggs or chicks in the nest when it was the only female present at the nest 6 days before the eggs were laid or if the male and female were seen consistently at the nest after egg laying.

We determined if females fought for the best quality nests by comparing nest quality codes where fights occurred with a comparison nest. Comparison nests were chosen as the closest nest with no eggs or chicks, occupied by a female with no cuts or blood that was not seen fighting during that season. The nest quality score ranged from "1" (poorest, nests which consisted of a scrape with no roof cover) through "5" (best, nests well covered; see Stokes and Boersma 1998, Renison et al. 2002).

The benefits of winning a fight can be measured as the increase in fitness as a result of winning (Grafen 1987). We quantified the benefits of winning by comparing between winners and losers three variables related to fitness: nest ownership, nest quality, and number of chicks fledged. If fighting ability and parental quality were positively associated, this would confound results as higher reproductive success would not necessarily result from winning. We determined whether fighting ability and parental quality were associated by comparing breeding success of winners and losers that had nests of similar quality, and by comparing egg volume of winners and losers. Egg volume is a good predictor of female parental quality (Reid and Boersma 1990).

For comparison of fight characteristics between sexes we chose 23 male-male and 23 female-female fights that were of similar duration (≤5 s) and which were matched for nest quality and date (≤4 days). To determine if size, body condition, and ownership were important for winning fights we calculated a body size index as the first factor extracted from a principal component analysis of body measurements. We calculated a body condition index as the standardized residuals from the linear regression of the first factor extracted from a principal component analysis of body measurements and body weight (Yorio

and Boersma 1994, Hood 1996). A female was classified as the nest owner if it was the parent of the eggs laid in the nest during the previous breeding season.

For statistical analysis we pooled data for all seasons. Fight duration (ANOVA: $F = 0.41$, df = 3, $P = 0.75$), length of cuts (Kruskal Wallis ANOVA: $\chi^2 = 2.054$, df = 3, $P = 0.56$), body size ($F = 0.96$, df = 3, $P = 0.42$), and body condition ($F = 1.33$, df = 3, $P = 0.27$) were similar among seasons, and all results had similar trends when analyzed for each season separately. We used paired statistical comparisons (paired sign, Wilcoxon, and *t*-test) when comparing winners with losers, and contested with comparison control nests. We randomly deleted fights where individuals or nests were sampled more than once (8 out of 55 fights). Complete information did not exist for all fights so sample sizes varied depending upon the test. For example, six fights had started by the time we arrived so fight duration was not known. We did not measure eggs of one or both contestants in 12 fights because eggs disappeared before we visited the nest or were never laid, and we knew nest ownership in the previous season for only 10 pairs of female opponents. Female-female fights were rare after the onset of incubation so we excluded the five fights we observed after the onset of incubation (October 20).

RESULTS

We observed 47 independent female-female fights. Females always fought over nests where a male and a female already were present. A female entered the nest site and began to vocalize at the female in the nest and tried to peck at her. Males did not peck or push the intruding female but often vocalized with one or both of the females. Most of the fights took place inside nests with females trying to push and bite each other. Fights lasted ≤56 min and eventually one female would leave the nest. On 36% of the occasions (17 of 47 fights) the female that left the nest re-entered the nest and continued to peck and push at the female in the nest. The male pecked at the losing female only when it was clear who the winner was.

Females fought from mid-September when they arrived at Punta Tombo. Female fights peaked during the first ten days of October at the start of egg laying (mean fights/h = 0.26 ± 0.08 SE). Females did not fight during incubation. A second small peak of fighting occurred after incubation for a 10-day period in mid-December (mean fights/h = 0.13 ± 0.07 SE), exclusively in nests without eggs or chicks.

Females fought in nests which were of better quality (mean nest quality score = 4.19 ± 0.13 SE) than comparison nests (mean score = 3.65 ± 0.13 SE; Wilcoxon paired test: $n = 47$, $Z = 3.66$, $P < 0.001$). Ninety-eight percent of the winners stayed in the contested nest while 85% of the losers moved to an alternative nest ($n = 47$ winners and losers; sign test: $P = 0.067$). Loser nests were of poorer quality than the nests for which they fought (mean nest quality scores: 4.37 ± 0.11 SE for winners, 3.43 ± 0.18 SE for losers; Wilcoxon paired test: $n = 47$, $Z = 3.66$, $P < 0.001$). Winners fledged more chicks (mean = 0.60 chicks ± 0.10 SE) than losers (mean = 0.31 chicks ± 0.08 SE; $n = 47$, $Z = 1.92$, $P = 0.047$). Winners and losers in nests of identical quality had similar reproductive success (winners fledged a mean of 0.47 chicks ± 0.17 SE, losers 0.53 chicks ± 0.19 SE; Wilcoxon paired test: $n = 15$, $Z = 0.22$, $P = 0.82$). Egg volume was similar between winners and losers (mean egg volume score for winners = 332.9 cm^3 ± 7.8 SE, mean for losers = 314.9 cm^3 ± 9.9 SE; paired *t*-test: $t_{34} = 1.33$, $P = 0.19$).

Female-female fights were less common than male-male fights (47 versus 138; $\chi^2 = 44.7$, df = 1, $P < 0.001$). Female-female fights were longer than male-male fights (Kolmogorov-Smirnov test: $Z = 2.97$, $P < 0.001$). When comparing female and male fights paired by fight length, nest quality, and date, we found that females received fewer flipper hits and shorter length of cuts than males (Table 1). Body size did not differ significantly between winners and losers (mean body size score for winners = 0.17 ± 0.25 SE, for losers = −0.07 ± 0.28 SE; paired *t*-test: $t_{46} = 1.18$, $P = 0.50$). Winners were in better physical condition than losers (mean body condition score for winners = 0.07 ± 0.05 SE, for losers = −0.02 ± 0.03; $t_{43} = 2.53$, $P = 0.008$). The difference in physical condition between opponents was not significantly correlated to fight length (Spearman correlation: $n = 41$, $r_s = 0.15$, $P = 0.36$). We knew the ownership

TABLE 1. During fights, female Magellanic Penguins received fewer hits and smaller cuts than males. Values are means ± SE.

	Females (n = 23)	Males (n = 23)	Wilcoxon paired test	
			Z	P
Flipper hits	1.39 ± 0.51	5.00 ± 1.76	2.045	0.039
Length of cuts (cm)	1.01 ± 0.21	3.98 ± 0.34	4.167	0.001

status of both contestants in 10 of the 47 fights. Nest owners won more fights (n = 8) than intruders (n = 2; binomial test: P = 0.055). Owners were in better physical condition in 9 of the 10 cases (binomial test: P = 0.011).

DISCUSSION

Female Magellanic Penguins fought over good quality nests during most of the breeding season, with two peaks of fighting: before and after egg laying. Fighting over nest sites or breeding territories before egg laying is well documented in penguins (Trivelpiece and Volkman 1979, Waas 1991) and other bird species such as male Purple Martins (*Progne subis*; Stutchbury 1991) and female European Starlings (*Sturnus vulgaris*; Sandell and Smith 1997). Because fights after egg laying were so few, we could not test why female Magellanic Penguins fought then even though they could not reproduce that season. However, in a related study in male Magellanic Penguins we found that fights after egg laying occurred mostly in nests without eggs or chicks which were of better quality than control nests, and male winners used the nest during the next breeding season (Renison et al. 2002). We believe that females also fight at the best nests after egg laying to establish ownership for the next breeding season. As males always were present at nests where females fought, females may be fighting for both a good quality nest and a good quality mate as well.

We found that on average female winners bred in higher quality nests and had higher reproductive success. Our results support the hypothesis that the difference in reproductive success between winners and losers could be due to the outcome of the fight (nest and mate acquisition) and not solely to preexisting differences in female quality. Egg size (an indicator of female quality; Reid and Boersma 1990) of winners and losers was similar, and when female opponents obtained nests of similar quality their reproductive success was similar. This suggests that winning makes a difference, and the quality of nests or mates may be the most important variables. Female physical condition before egg laying, however, is an important determinant of reproductive success (Yorio and Boersma 1994). Winners were in better physical condition than losers and therefore the difference in reproductive success between winners and losers probably also reflects the physical condition of the females.

Females were 9% less likely than males to return to our study area in the following year, suggesting that they may have lower survival or lower nest fidelity than males, and as a consequence there were more nests and mates available to females (Renison 2000). For fights before egg laying, 82% of the male winners and 40% of the male losers later were found breeding (Renison et al. 2002), while for females the percentages were 98% and 85%, indicating that females were more likely to find a nest or attract a mate. The relative benefits of winning a nest, therefore, were less for females than for males, and as predicted females fought less frequently and their fights were less intense than male-male fights. However, female–female fights were longer than male-male fights, perhaps because they were less intense. When females fought they pushed and pulled each other while inside the nest but were constrained by the burrow and could not use their flippers to hit their opponent. The total length of their cuts were shorter than when males fought.

Body condition and previous ownership of a nest predicted the outcome of female fights, while body size did not predict outcome. Body condition before egg laying may be important because females take the first incubation shift and need to fast until the male returns. Hence, females in better body condition

are more likely to be successful breeders (Yorio and Boersma 1994). Ownership may be important, because penguins that switch nests or mates have lower reproductive success (Fowler 1993). Hence, it is possible that body condition and ownership were good predictors of outcome *per se* or because they were associated to an asymmetry in resource value and females which were more likely to be successful breeders were more motivated to win.

In females, body condition, ownership, mate fidelity, and winning were strongly associated, suggesting that females may win because of all or some combination of these factors. We could not test which variable was the ultimate cause of female winning because they were strongly associated and we could not test them separately. However, if body condition *per se* is important in winning fights, when differences in body condition between contestants are small, fight duration should increase (Parker 1974, Enquist and Leimar 1983), which did not occur. The rule "owners win" is predicted to be an ESS only when benefits of winning are low, which did not appear to be the case for female Magellanic Penguins as winners fledged more chicks. This leaves us with the "asymmetry in resource value" hypothesis explaining who wins female fights. Differences in resource value between owners and intruders have been documented in Pied Wagtails (*Motacilla alba*; Davies 1981). Consistent with this interpretation, the male Magellanic Penguins did not interfere in the fights until the outcome was clear. They are likely to benefit by having a female which is in better body condition. Female fights may be longer not only because their fights are less damaging, but also because intruders need to be sure owners are highly motivated and can not be easily repelled.

We conclude that fighting in female Magellanic Penguins is less frequent than in males probably because females have less to lose by being expelled from a nest. Nevertheless, there is a cost. The small increase in reproductive success of females holding higher quality nests ensure that females, like males, will fight for high quality nests. Body condition and ownership were good predictors of winning, possibly because females in better body condition and which had bred in the nest the previous season are more motivated as nests are more valuable to them.

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